

A new genus and species of aquatic gastropods (Rissooidea: Hydrobiidae) from the North American Southwest: phylogenetic relationships and biogeography

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Abstract.—*Juturnia*, a new genus composed of three species from the Rio Grande region of southwestern North America, is described. Two of these species were previously placed in the genus *Durangonella* while the third, *J. tularosae*, is described herein. *Juturnia* is shown to be a monophyletic subunit of the gastropod subfamily Cochliopinae based on phylogenetic analysis of mitochondrial DNA sequences and an uniquely shared morphological character (within the subfamily), the presence of a single non-glandular lobe on the inner edge of the penis. Our phylogenetic hypothesis indicates that *Juturnia* is most closely related to North American brackish-coastal taxa, and we conjecture that progenitors of this genus penetrated inland along the Tertiary drainages which headed along eastern flanks of Laramide uplifts and flowed to the Gulf of Mexico. Subsequent vicariance of congeners in southeastern New Mexico is attributed to development of the Pecos depression, and inception of the drainage divide between the Rio Grande Rift and southern Great Plains.

While various hypotheses have been proposed to explain the distributions of aquatic biota in the Rio Grande region of southwestern North America, these have been hampered by a paucity of pertinent phylogenies (Smith & Miller 1986). Cochliopinid (= littoridinid) gastropods form a diverse component of this biota and also are of interest because of their high level of local endemism (Taylor 1966, 1987). Recent phylogenetic reconstructions based on analysis of mitochondrial DNA sequences suggest that this fauna includes several lineages derived from marine or brackish water coastal progenitors (Liu et al. 2001), and that inland snail distributions reflect vicariant events which preceded establishment of modern regional topography (Hershler et al. 1999, 2002). Herein, we describe a newly recognized monophyletic group of coch-

liopinids whose distribution, habitat, and systematic relationships provide an additional perspective on the biogeographic history of this region.

Materials and Methods

This report primarily is based on material deposited in the National Museum of Natural History, Smithsonian Institution (USNM). Relevant type material from the Natural History Museum, London (BMNH) also was studied. Specimens of the new species were relaxed in the field with menthol crystals, and then fixed in dilute formalin (10% of stock solution) and preserved in 70% ethanol. Prior to dissection, shells were removed from animals by soaking in dilute hydrochloric acid. Animals were dissected using a WILD M8 research

microscope and drawings were made with the aid of a camera lucida attachment. Live specimens were studied for description of head-foot and penis. Methods of preparation of material for scanning electron microscopy are of Hershler (1998). Counts of radular cusps and tooth rows were determined from scanning electron images. Terminology of anatomical features follows Hershler (2001) and character state delineations are from Hershler & Ponder (1998). Institutional abbreviations follow Leviton et al. (1985).

Partial sequences of the mitochondrial cytochrome c oxidase subunit I (mtCOI) gene were obtained from two specimens of the new species using methods of Liu et al. (2001) (Genbank accession number AF474371). Sequences were utilized for phylogenetic analysis along with previously analyzed mtCOI sequences of members of cochliopine sub-clades III, IV and V (Liu et al. 2001; also see Hershler et al. 1999), which represent the portion of the subfamily topology that contained previously described species which we allocate herein to *Juturnia*. In this earlier analysis, sub-clade V was sister to the lineage containing species of *Juturnia* and thus we used its most basal member (*Mexipyrgus carranzae*) for rooting in the current study. Analyses were conducted using the maximum parsimony, maximum likelihood, and minimal evolution options of PAUP*4.0 (Swofford 2000) following Liu et al. (2001). Bootstrapping (Felsenstein 1985) with 1000 replications was performed to assess branch support on the resulting trees. Timing of branching events was estimated using the fossil-based calibration for mtDNA third position transitions (3–4% per My) and transversions (0.42% per My) for the marine gastropod genus *Nucella* (Collins et al. 1996) and may be accurate only to the extent that evolutionary rates are comparable among mitochondrial genes and among muricid and cochliopine gastropods.

Systematics

Family Hydrobiidae Troschel, 1857
Subfamily Cochliopinae Tryon, 1866

Juturnia, new genus

Type species.—*Durangonella coahuilae* Taylor, 1966, by original designation. Other species included are *Tryonia kosteri* Taylor, 1987, and *Juturnia tularosae*, new species (described below).

Diagnosis.—Shell ovate-conic to turritiform, small to medium-sized (2.0–5.1 mm shell length), grey-white or clear, transparent. Periostracum thin, light tan to brown. Protoconch of 0.7–1.0 whorl, planispiral or depressed trochiform, surface corrugated but without microsculpture. Teleoconch of 4.0–8.5 slightly to strongly convex whorls. Teleoconch sculpture of closely spaced orthocline or weakly prosocline growth lines, fine spiral striae sometimes present and crossed by growth lines. Aperture ovate, inner lip thin to slightly thickened, broadly adnate to completely separated from parietal wall, outer lip thin or slightly thickened. Umbilicus rimate to broadly open. Operculum thin, multispiral, with eccentric nucleus.

Central radular teeth with weak to moderately indented dorsal edge; 3–6 lateral cusps on each side; 1 pair of basal cusps, basal process V-shaped. Lateral radular teeth with straight to slightly indented dorsal edge; lateral shaft much longer than dorsal edge; 3–5 cusps on inner side; 4–7 cusps on outer side. Inner marginal teeth with 23–33 cusps, outer marginal teeth with 21–34 cusps.

Animal moderately pigmented, eyes pigmented. Cephalic tentacles with dorsal and ventral longitudinal ciliary tracts and transverse tracts along outer edge of basal portion of left tentacle. Ctenidium well developed and wide, extending most of to entire length of pallial cavity. Osphradium located near middle of ctenidium, narrow to ovate. Renal organ with short pallial section; renal organ longitudinal, renal opening slightly muscularized. Pericardium with short pal-

lial section; short efferent vessel between anterior end and posterior end of ctenidium or ctenidium overlapping anterior end of pericardium. Posterior stomach slightly smaller than anterior chamber; single digestive gland opening; small posterior caecum present or absent; style sac about as long as remaining portion of stomach.

Testis of vertical compound lobes, occupying most of visceral coil behind stomach and partly overlapping posterior stomach chamber. Seminal vesicle beneath anterior portion of testis, coiled on digestive gland behind stomach. Prostate gland extends into pallial roof for 33–67% length, narrow-pyriform. Visceral vas deferens opens to ventral edge of prostate gland from near posterior edge to 33% anterior from edge. Pallial vas deferens opens to ventral edge of prostate gland slightly behind anterior edge, initial portion weakly recurved, remainder straight or weakly undulating. Penis elongate-rectangular with little taper; distal end blunt to evenly rounded, with sub-terminal papilla, generously ciliated; inner edge with small narrow-triangular lobe positioned at about 67% of length from base. Penial duct straight distally, near straight to moderately undulating in basal portion.

Ovary simple, occupying very small part of visceral coil ($\leq \frac{1}{4}$ whorl). Proximal coiled oviduct narrow, thin-walled; distal portion broader, with posterior-oblique bend or weak coil, usually containing sperm. Coiled oviduct and seminal receptacle duct joined by very short duct at point where former opens to posterior edge of albumen gland. Bursa copulatrix small, horizontally ovate or cylindrical, positioned well anterior to posterior edge of brood pouch; duct opening from anterior edge of pouch, narrow to medium width. Seminal receptacle small to medium-sized, sub-globular, abutting left side of bursa copulatrix; duct opening from anterior edge of pouch, very short. Sperm duct narrow, posterior section with weak bend or kink, anterior portion straight, opening to ventral edge of spermathecal

duct a little in front of posterior wall of pallial cavity. Albumen gland very small, abutting right side of bursa copulatrix. Female ovoviviparous, with small to medium number of embryos brooded in large, thin-walled capsule gland. Brood pouch posteriorly folded, folded section narrow, ventral; anterior opening terminal, muscularized, slightly recurved. Spermathecal duct narrow to medium width, opening a little behind brood pouch opening.

Remarks.—The two previously described species that we allocate to *Juturnia* most recently were placed in the genus *Durangonella* (Hershler 2001). *Durangonella* Morrison, 1945 was erected for four species from central Mexico which have smooth, elongate-conic shells. Morrison (1945) re-described the type species, *Hydrobia seemani* Fraunfeld, 1863, and described the other three congeners from empty shells. Morrison presented but few details of soft parts, based on study of dried material of the type species, and the only anatomical criterion by which he distinguished *Durangonella* from closely similar *Tryonia* was its “different pattern” of penial ornament (Morrison 1945:18–19). A fifth species of *Durangonella* (*D. coahuilae*) subsequently was described from Chihuahuan Desert shells (Taylor 1966) and a sixth congener (*D. kosteri*), from the Pecos River basin, recently was transferred to the genus (Hershler 2001). The two northern congeners (*D. coahuilae*, *D. kosteri*) have been shown to be members of the hydrobiid subfamily Cochliopinae, within which they form a distinct group united by a unique suite of anatomical character-states (Hershler 2001). They also have been shown to form a well supported cochliopine sub-clade based on mtDNA sequences (Liu et al. 2001). However, trenchant characterization of *Durangonella* has been prevented by a paucity of information for southern congeners, none of which has been further studied since Morrison’s (1945) work.

The type species of *Durangonella*, *Hydrobia seemani* Fraunfeld, 1863, was de-

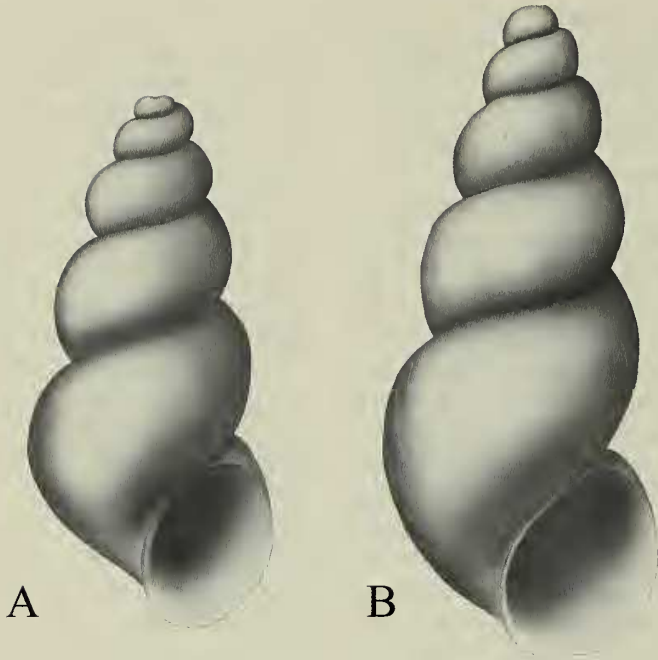


Fig. 1. Shells of *Durangonella seemani*. A. Durango City, Durango (USNM 251826). B. Syntype, Durango, N.W. Mexico (BMNH 20001099). Shell "A" is 3.02 mm tall; shell "B" is printed to the same scale.

scribed from shells collected in "Durango, N.W. Mexico" by Berthold Seemann during his tenure as naturalist aboard the H.M.S. Herald. Presumably Seeman made this collection in 1849 or 1850 when he left the vessel, ventured inland from the Pacific Coast, and visited the city of Durango and nearby areas. However, neither his expedition narrative (Seeman 1853) nor his resulting botanical monograph (Seeman 1852-7) mention this collection. Frauenfeld (1863:1025; English translation in Morrison 1945:19) briefly described the shell of this species, emphasizing its slender and conical shape, deep suture, small aperture, and simple lip; and subsequently illustrated a specimen (Frauenfeld 1865, fig. 8). Morrison (1945) redescribed this species from specimens that botanist Edward Palmer collected (probably in 1896 fide USNM accession papers; and field itinerary [McVaugh 1956]) from a spring that then provided the domestic water supply to Durango City. Shells of this sample (USNM 251826, Fig. 1a)

closely resemble syntypes of *H. seemani* (Fig. 1b) and are presumed by us to be conspecific, although they are not assuredly topotypes as Morrison (1945:19) claimed. Recently we examined rehydrated specimens from USNM 251826 and determined that Morrison's (1945, fig. 5) description was in error as the male penes do not have simple lobes but instead are ornamented with glandular papillae (Fig. 2). We also observed in dissection that the female spermathecal duct (= sperm tube) of these snails opens a little in front of the posterior wall of the pallial cavity which, together with penial morphology, indicates that this snail belongs to the genus *Tryonia* (fide Hershler 2001). This is consistent with ongoing field surveys in the Durango region which have yielded snails with *Tryonia*-like anatomy (Hershler unpublished).

Based on these new observations (made subsequent to the recent synopsis of *Durangonella*; Hershler 2001), we conclude that *Durangonella* Morrison, 1945 (type

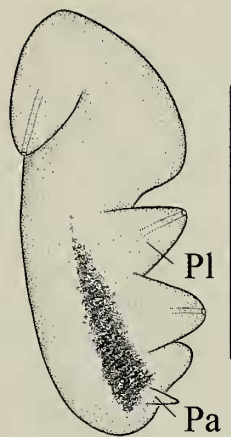


Fig. 2. Penis of *Durangonella seemani*, USNM 251826; scale equals 0.5 mm. Abbreviations—Pa, terminal papilla; Pl, penial lobe.

species, *Hydrobia seemani*) is a junior subjective synonym of *Tryonia* Stimpson, 1865. Accordingly, we have erected a new genus (*Juturnia*) for the two species from the northern Chihuahuan Desert and Pecos River basin which previously were assigned to *Durangonella*, but which are well-differentiated from *Tryonia* and other cochliopine genera. The three other species of *Durangonella* (all from central Mexico) cannot confidently be assigned to genus because they are known only from shells and because the regional hydrobiid fauna remains poorly known. These species are “*Durangonella*” *dugesiana* Morrison, 1945 (type locality, Andocutin, Guanajuato; fide Taylor 1966); “*D.*” *mariae* Morrison, 1945 (one meter below the present surface of the dry bed of the lake at Tlahuac, 20 kilometers east of Xochimilco, Distrito Federal); and “*D.*” *pilsbryi* Morrison, 1945 (Paso del Rio, Colima).

The shells of *Juturnia* broadly overlap in size, shape, and sculptural features with those of several other epigeic cochliopines of southwestern North America (*Eremopyrgus*, *Littoridinops*, *Pseudotryonia*, *Tryonia*). Among these taxa *Juturnia* shares with *Littoridinops* and *Pseudotryonia* an elongate sperm duct which opens to the spermathecal duct in the posterior pallial cavity.

(Other similar-shelled regional cochliopines have a coiled sperm duct positioned entirely behind the posterior wall of the pallial cavity; Hershler 2001.) *Juturnia* differs from these two genera and all other members of subfamily in having a single, non-glandular lobe on the inner edge of the penis, which may be a synapomorphy for the genus. *Juturnia* is further distinguished from other regional cochliopines by its sub-globular seminal receptacle, weakly coiled renal oviduct, and storage of sperm in the coiled oviduct.

Our phylogenetic analyses of mtCOI sequences (all of which resulted in the same tree topology) provided good (73%) support for monophyly of *Juturnia* (Fig. 3). Within this topology *Juturnia* was placed within a poorly supported clade that also contained two other genera which have an elongate sperm duct (*Littoridinops*, *Spurwinkia*) and *Pyrgophorus*, which has a coiled sperm duct.

Distribution.—Lower Rio Grande region (Fig. 4). *Juturnia kosteri* is distributed along the lower Pecos River, a major tributary to the lower Rio Grande. *Juturnia coahuilae* lives in the Cuatro Ciénegas basin (Coahuila, Mexico), whose northeast portion drains to the headwater region of the Rio Salado (Minckley 1969), which also is tributary to the lower Rio Grande. *Juturnia tularosae* (described below) lives in a hydrographically closed basin in the southern Rio Grande rift.

Habitat.—Spring-fed water bodies, typically consisting of headsprings and their stream outflows. *Juturnia coahuilae* also lives in Laguna Grande, the terminus of a spring-fed drainage system (Hershler 1985). Waters inhabited by congeners range from near freshwater to hypersaline (e.g., Laguna Grande [=Laguna Salada], 309 g/l total dissolved solids; Minckley & Cole 1968). Snails are benthic and typically live in soft sediments.

Etymology.—From N. Latin *Juturna*, the Roman goddess of wells and springs. Gender feminine.

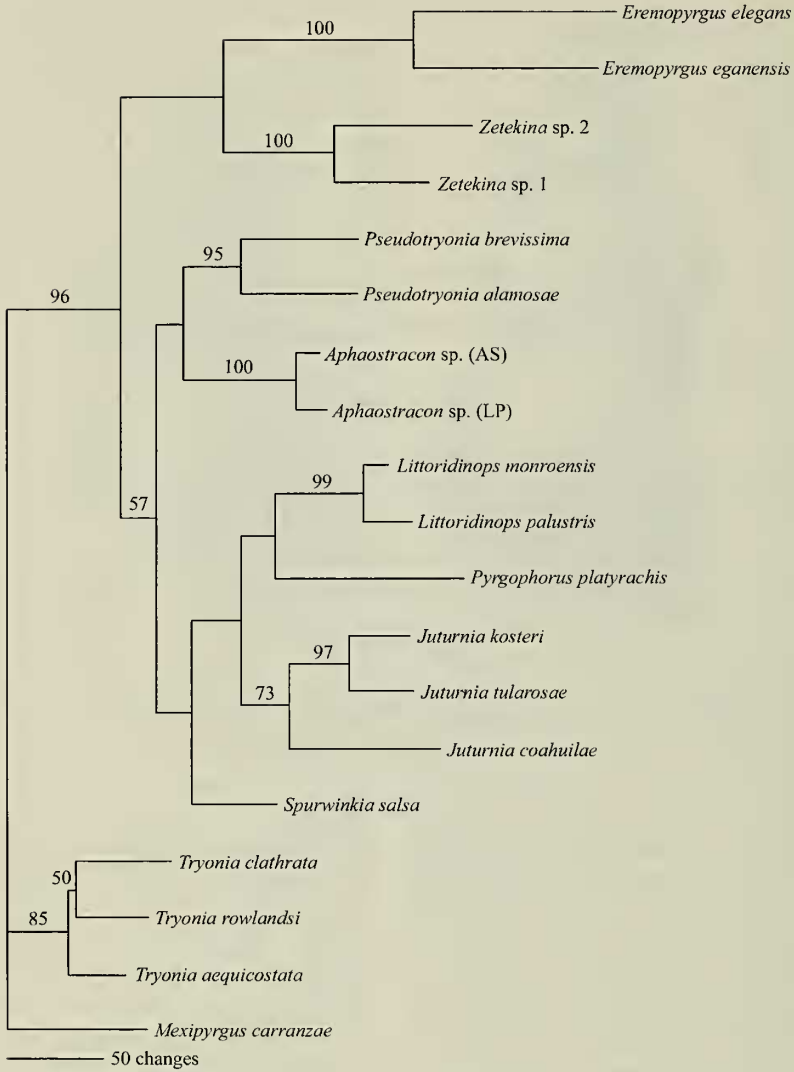


Fig. 3. Single shortest length tree based on maximum parsimony analysis of mtCOI sequence data. CI, 0.57; TL, 1473. Bootstrap percentages are given when >50%. The two specimens of *J. tularosae* were identical in their sequences. Samples of *Aphaostracon* sp. were from Alexander Springs, Lake Co, FL (AS); and Lake Panasoffkee, Sumter Co., FL (LP). Data for species other than *J. tularosae* are from Hershler et al. (1999) and Liu et al. (2001).

Juturnia tularosae, new species
Tularosa juturnia

Diagnosis.—A small to medium-sized *Juturnia* which differs from congeners in shell having more convex teleoconch whorls (which frequently are shouldered); and female genitalia having smaller bursa copulatrix and narrower spermathecal duct.

Description.—Shell (Fig. 5A, B) ovate-

conic, width/height 57–80%, with convex spire sub-equal to shell width, 1.70–4.84 mm tall, whorls 4.0–6.0. Periostracum light tan. Protoconch of about 0.75 whorl, surface slightly roughened to corrugated (Fig. 5C, D). Teleoconch whorls highly convex, evenly rounded or wider above than below, smooth apart from well-developed growth lines and occasional weak spirals, shoulders

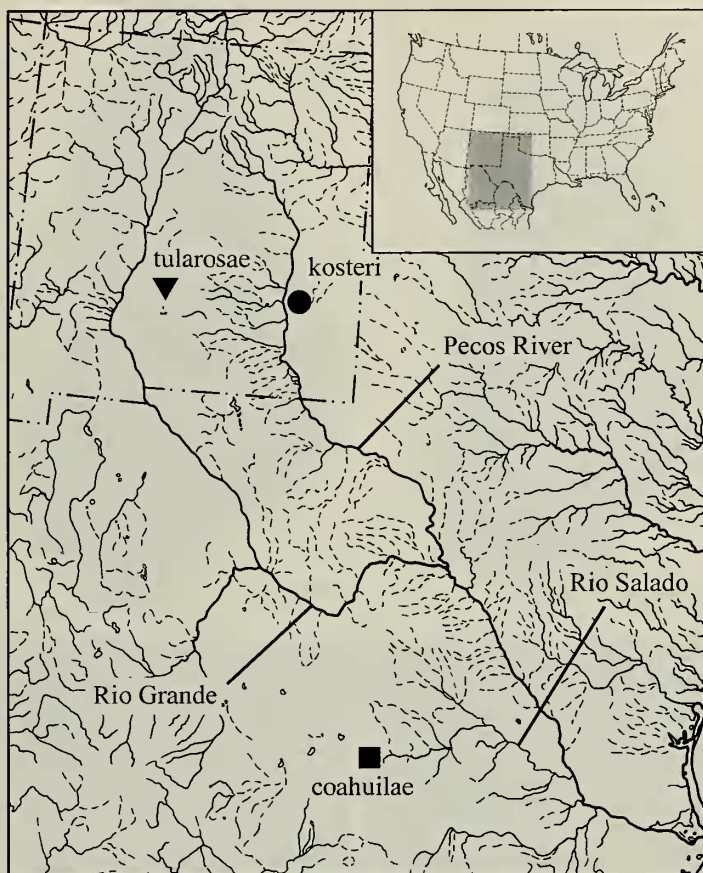


Fig. 4. Drainage map of Rio Grande basin and adjacent areas showing distribution of *Juturnia*.

often well-developed. Teleoconch sometimes with weak demarcation at 1.25–1.75 whorl whorls reflecting cessation of growth in brood pouch. Aperture medium-sized. Inner lip thin or slightly thickened, straight or weakly rounded, usually complete and narrowly or broadly adnate across parietal wall, sometimes narrowly disjunct; lip sometimes narrowly reflected in columellar region. Outer lip orthocline or weakly procline, straight or weakly sinuate. Larger specimens often having last 0.25–0.5 whorl loosened from body whorl. Umbilicus rimate to broad. Females larger than males, but having similarly shaped shells (Fig. 6, Table 1). Shell parameters are in Table 1.

Operculum flat or slightly concave, ovate, light amber. Outer side nearly smooth, edges of later whorls weakly frilled

(Fig. 7A). Attachment scar margin slightly thickened on inner side; outer margin very weakly rimmed (Fig. 7B).

Radula with about 53 well-formed rows of teeth; ribbon length, 579 μm ; ribbon width, 120 μm ; central tooth width, 24.8 μm . Dorsal edge of central teeth moderately indented, basal process usually rounded below, base even with lateral margins, median cusps slightly longer than laterals, pointed or rounded distally; lateral cusps 4–5; basal cusps small (Fig. 8A). Lateral teeth having 3–4 cusps on inner side and 6–7 cusps on outer side; outer wing well-flexed, curved, length 210–240% width of tooth face; central cusp pointed or rounded distally, dorsal edge weakly concave; basal tongue moderately developed (Fig. 8B). Inner marginal teeth with 26–33 cusps, cutting edge on

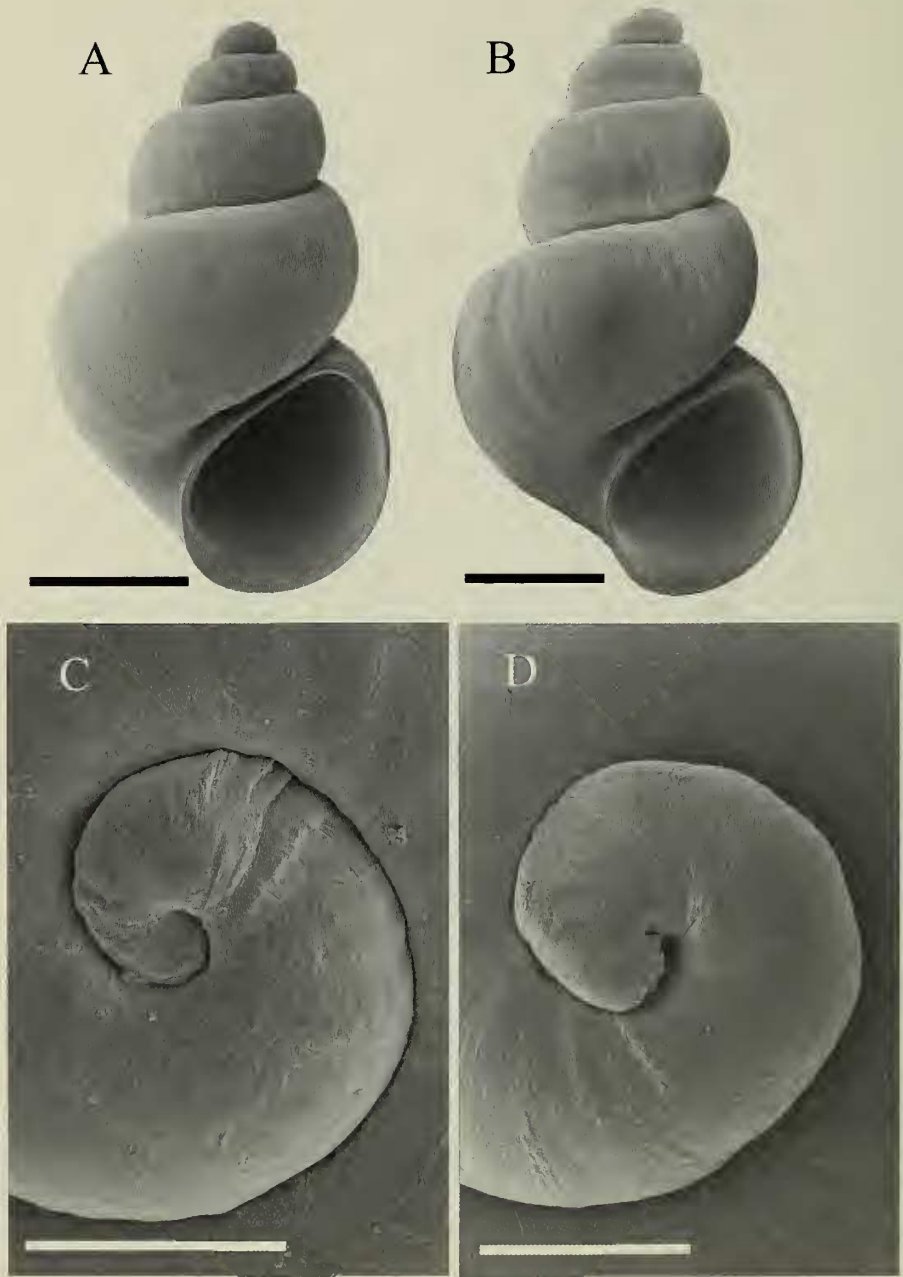


Fig. 5. Scanning electron micrographs of shells of *J. tularosae*, USNM 894803. A, B. Variation in shell shape; scales equal 1 mm. C, D. Variation in protoconch appearance; scales equal 100 μm .

outer side of tooth, occupying ca. 33% of tooth length (Fig. 8D). Outer marginal teeth with 26–33 cusps, cutting edge on inner side of tooth, occupying ca. 30% of tooth length (Fig. 8E). Cusps on inner marginal

teeth larger than those on outer marginals (Fig. 8C).

Snout dark grey or black. Cephalic tentacles light-medium grey, sometimes darker near bases and often having a black patch

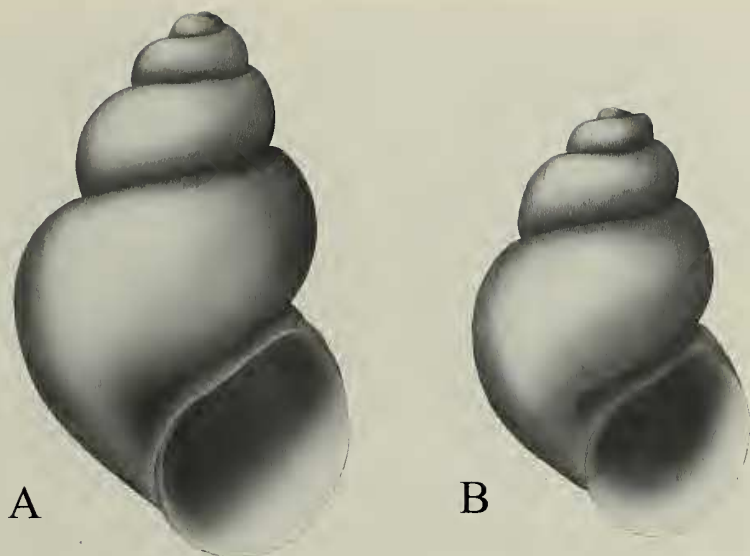


Fig. 6. Shells of *J. tularosae*. A female (holotype), USNM 894737. B, male, USNM 854956. Shell "A" is 3.77 mm tall; shell "B" is printed to the same scale.

near distal tips. Yellow granules scattered along tentacle length, with dense white patch of granules clustered on neck. Foot dark grey, with numerous embedded clear-white granules. Mantle, visceral coil grey-black, pigment particularly dark over testis. Distal penis having large grey-black patch of melanic pigment; proximal portion pigmented with numerous yellow granules.

Snout rectangular, distal lips slightly expanded. Tentacles narrow, ca. 150% length of snout (while animal crawling), slightly

tapered, with rounded tips. Base of tentacles without pronounced eyelobe. Foot ca. 250% longer than wide; lateral wings well-developed; anterior edge slightly convex.

Ctenidium extending to near mantle edge and overlapping pericardium posteriorly. Ctenidial filaments ca. 27, extending to near rectum, narrowly triangular with apices positioned slightly to left of mid-line; lateral surfaces having well developed ridges. Hypobranchial gland weakly developed alongside rectum in posterior pallial cavity. Os-

Table 1.—Shell measurements of holotype (USNM 894737) and paratypes (USNM 894741) of *Juturnia tularosae*. *t* values are given for comparisons of means among sexes (95% confidence level). *Sexual dimorphism significant ($P < 0.01$).

	SL	SW	LBW	WBW	AL	AW	TW	SW/SL
Holotype	3.14	1.87	2.26	1.75	1.27	1.15	4.75	0.59
Paratypes								
♂ ($n = 22$)								
\bar{X}	2.44	1.61	1.77	1.41	1.03	0.97	4.55	0.66
SD	0.23	0.13	0.15	0.11	0.09	0.08	0.24	0.03
♀ ($n = 30$)								
\bar{X}	2.91	1.92	2.06	1.69	1.20	1.14	4.90	0.67
SD	0.36	0.14	0.22	0.15	0.12	0.09	0.25	0.04
<i>t</i>	5.81*	8.46*	5.63*	7.65*	6.17*	7.16*	5.17*	0.260

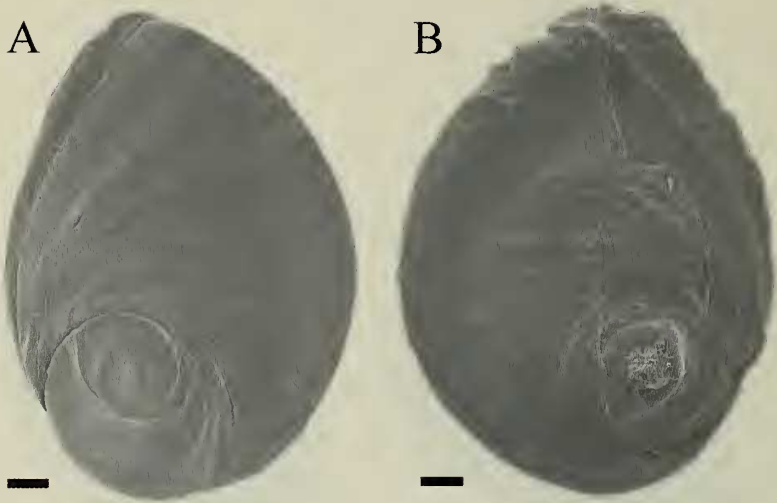


Fig. 7. Scanning electron micrographs of opercula of *J. tularosae*, USNM 894803; scales equal 100 μ m. A. outer side. B. inner side.

phradium ovate, positioned slightly posterior to middle of ctenidial axis. Renal organ narrow. Style sac about as long as remaining portion of stomach, posterior caecum of stomach small, triangular.

Testis 1.0–1.25 whorl, slightly overlapping posterior stomach chamber. Seminal vesicle consisting of a few coils. Prostate gland small, yellow, bean-shaped, 50–67% of length in pallial roof, ovate in section, walls thickened all around (Fig. 9). Visceral vas deferens opening near posteroventral edge of pallial gland; pallial vas deferens straight or weakly kinked proximally on columellar muscle. Penis medium-sized, straight or slightly curved; distal portion well expanded in living specimens (Fig. 10A), evenly rounded or weakly expanded in preserved material (Fig. 10B). Narrow penial duct straight, or weakly undulating in middle section.

Ovary positioned slightly behind stomach. Distal genitalia shown in Fig. 11. Renal oviduct loop (Ro) posterior-oblique, bulging with sperm. Bursa copulatrix (Bu) ovate, sometimes weakly pigmented, positioned a little behind posterior pallial wall, duct (Dbu) narrow. Seminal receptacle (Sr) small, abutting anterior portion of bursa co-

pulatrix. Sperm duct (Sdu) kinked posteriorly, otherwise straight. Duct to albumen gland (Dag) issuing from oviduct slightly distal to coiled section. Spermathecal duct (Sd) narrow, although broadening distally, opening slightly raised. Albumen gland (Ag) abutting the ventro-right lateral surface of the bursa copulatrix. Brood pouch (Bp) containing 2–5 shelled embryos; an additional series of weakly developed embryos often present in posteriorly folded section. Anterior opening of brood pouch (Obp) muscular, raised, positioned alongside anus.

Type material.—A live-collected series obtained by Craig Stockwell on 4 Feb 2001 from Salt Creek at Range Road 316 crossing, White Sands Missile Range, Tularosa basin, Sierra County, New Mexico, Township 12S, Range 6E, NE 1/4 section 16. The holotype (USNM 894737, Fig. 5A) is a dried female from this series, while remaining specimens (also dried) are reposit as paratypes (USNM 894741). Three additional paratype series from the type locality were collected at other times during 1999–2001 (USNM 854956, USNM 894803, USNM 905339).

Other material examined.—Dried shells



Fig. 8. Scanning electron micrographs of radula of *J. tularosae*, USNM 894803; scales equal 10 μm . A. Central teeth. B. Lateral teeth. C. Portion of radula ribbon showing relative sizes of cusps on outer and inner marginal teeth. D. Inner marginal tooth. E. Outer marginal teeth.

from Salt Creek, in a canyon ca. 6.4 km above Range Road 316, Tularosa basin, Sierra County, New Mexico, Township 12S, Range 6E, NE 1/4 section 3 (USNM 894738).

Distribution and habitat.—*Juturnia tularosae* apparently is endemic to Salt Creek (Meinzer & Hare 1915, pl. VIII C), a major drainage of the northern Tularosa basin which heads in the San Andres and Oscura

ranges and is supported on the basin floor by the discharge of Salt Springs. A field survey during March, 2001 indicated that snails were restricted to a central reach of Salt Creek, extending from a canyon ca. 6.4 km north of Range Road 316 to ca. 0.5 km downflow from this road. The northern end of the snail range coincides with a waterfall (ca. 2 m high) at the head of this canyon.

During recent years (1995–1999) dis-

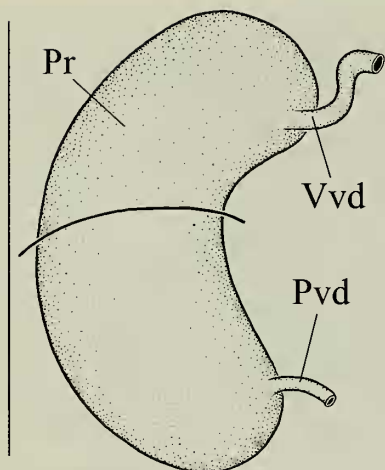


Fig. 9. Prostate gland (left side) of *J. tularosae*, USNM 894956; scale equals 0.5 mm. Abbreviations—Pr, prostate gland; Pvd, pallial vas deferens; Vvd, visceral vas deferens.

charge of Salt Creek in the vicinity of the type locality of *J. tularosae* averaged 32.28 liters/second (Ortiz & Lang 1996, Ortiz et al. 1997, 1998, 1999). During this time period the stream has been subject to periodic flooding, usually during the summer, with a maximum discharge of 1982.18 liters/second. Water temperature varied from 7.0–33.5°C; dissolved oxygen was typically high, with an average of 9.29 mg/liter; and pH was fairly constant, with an average of 8.07. Salt Creek is saline and both alkali-(Na and K) and chloride-rich. These water quality data are similar to those of earlier studies of Salt Creek (Meinzer & Hare 1915, Miller & Echelle 1975, Stockwell & Mulvey 1998).

Etymology.—A geographical name referring to endemism of this snail in Tularosa basin, southeast New Mexico.

Remarks.—This species, together with *J. kosteri*, is distinguished from *J. coahuilae* by its much broader shell (compare Figs. 5, 6 with Hershler 1985, fig. 33), less elongate bursa copulatrix, and more anteriorly positioned seminal receptacle (compare Fig. 11 with Hershler 1985, fig. 36). Our mtCOI-based tree (Fig. 3) was consistent with morphology in that the former two species

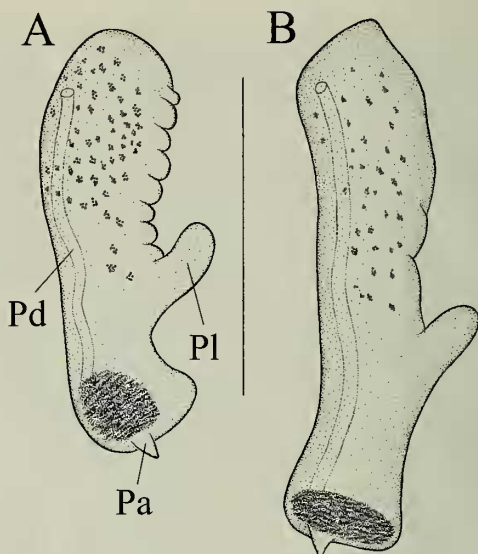


Fig. 10. Penes (left side) of *J. tularosae*; scale equals 250 μ m. A. Live specimen, USNM 894803. B. Formalin-fixed specimen, USNM 894956. Abbreviations—Pa, terminal papilla; Pd, penial duct; Pl, penial lobe.

formed a strongly supported (97%) subclade. In addition to the characters listed above (see Diagnosis) *Juturnia tularosae* differs from *J. kosteri* by the more deeply indented dorsal edge of the central radular teeth (compare Fig. 8A with Hershler 2001, fig. 12A), squatter shape of prostate gland, very short pallial extension of the female sperm duct, papilla-like opening of the brood pouch, and occasional pigment on the bursa copulatrix (compare Fig. 11 with Hershler 2001, fig. 13).

Discussion

The phylogenetic analysis of mtCOI sequences (Fig. 3) indicates that monophyletic *Juturnia* is more closely related to brackish water cochliopines confined to the western Atlantic and Gulf of Mexico margins (*Littoridinops*, *Pyrgophorus*, *Spurwinkia*) than to other taxa of southwestern North America (*Eremopyrgus*, *Mexipyrgus*, *Tryonia*) and is consistent with an origin associated with inland invasion by Gulf Coastal ancestors. These sequence data also suggest

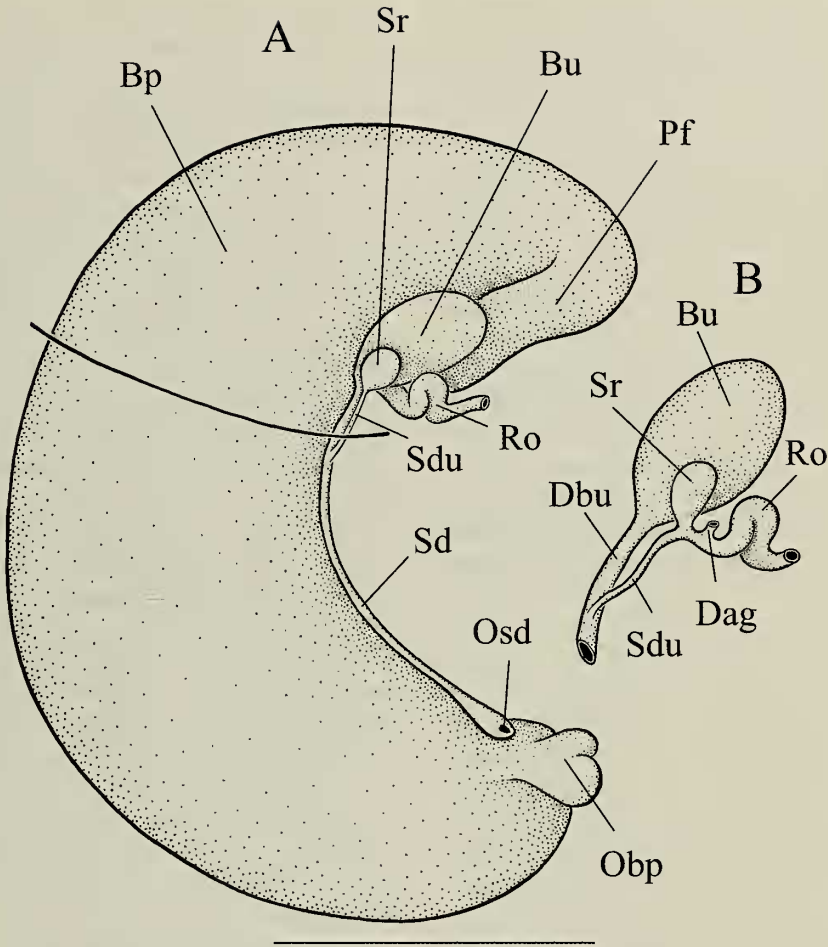


Fig. 11. Female genitalia (left side) of *J. tularosae*, USNM 894956; scale equals 500 μm . A. Brood pouch (Bp) and associated structures. B. Bursa copulatrix (Bu) and associated structures. Abbreviations—Bp, brood pouch; Bu, bursa copulatrix; Dag, duct connecting oviduct and albumen gland; Obp, opening of brood pouch; Osd, opening of spermathecal duct; Pf, posterior folded section of brood pouch; Ro, renal oviduct; Sd, spermathecal duct; Sdu, sperm duct; Sr, seminal receptacle.

that divergence of *Juturnia* occurred 4.3–14.9 Ma (Miocene-early Pliocene) and thus preceded assembly of the modern Rio Grande drainage, which was not completed until its master stream breached the Lake Cabeza de Vaca complex (sensu Strain 1966) in northeastern Chihuahua and northwestern Texas ca. 2.5–2.0 Ma (Gustavson 1991, Mack 1997, 2001) and subsequently penetrated to the sea. We conjecture that coastal progenitors did not penetrate inland through the Rio Grande but instead along the drainages which headed on the flanks of

Laramide uplifts (e.g., Rocky Mountains, Sierra Madre Orientale; Winker 1982, Galloway et al. 1991) and flowed east and southeast to the Texas Gulf Coast during the early-mid Tertiary (Thomas 1972, Belcher 1975, Belcher & Galloway 1977, Cather 1991, Christiansen & Yeats 1992). Note that the Rio Grande region has had a complex biogeographic history with respect to the Gulf of Mexico and other venues of inland transport of marine biota, which may have ranged from stranding of 'relicts' in conjunction with recession of Cretaceous

seas (Bowman 1981, Holsinger 1986) to Quaternary aerial dispersal on or in birds (Bachuber & McClellan 1977), also may have occurred.

Progenitors may have been euryhaline and capable of penetrating into freshwater environments (fide Hershler et al. 2002). Alternatively, ancestral snails may have been salt dependent in which case their inland dispersal was more tightly constrained by water chemistry. Taylor (1985:318–319) speculated that the Pecos River, which flows through a region having a long history of evaporite dissolution (Bachman 1976) and is highly mineralized along portions of its length (Gustavson & Finley 1985), functioned as an early saline conduit for coastal molluscan colonists into this region. Although we disagree with aspects of this interpretation of Pecos River history (see below), we note that the Rio Salado (to which *J. coahuilae* is endemic) also contributes a large amount of salt to the Rio Grande (Miyamoto et al. 1995) derived in part from dissolution of (Cretaceous) evaporites (Back et al. 1977, Lesser & Lesser 1988) and thus may have had a long brackish-saline history. (This river may date to the Paleocene; Galloway et al. 1991:302.) Note that *Assimineia pecos*, a member of a salt-adapted gastropod genus typically associated with coastal margins (Abbott 1958), is distributed (together with *Juturnia*) in upper segments of the Pecos River and Rio Salado basins (Taylor 1987), which further implies a close historical relationship between these areas and saline habitats.

We attribute vicariance of the *Juturnia* sub-clade in southeastern New Mexico (*J. kosteri* and *J. tularosae*) to the well documented capture of segments of the old drainage system which extended from the southern Rocky Mountains across the southern High Plains (Plummer 1933, fig. 51A) by the Pecos depression (fide Horberg 1949), which formed through dissolution of bedded Permian salt followed by regional subsidence (Gustavson & Finley 1985,

Gustavson & Winkler 1988). The closely proximate occurrence of marine-like biota in Great Plains drainage just east of the Pecos divide (Creel 1964) is congruent with this hypothesis. The timing of drainage diversion has not been well established, but presumably occurred following deposition of the regionally widespread Ogallala Formation, which ended ca. 3.5–5 Ma (Hawley 1993a). These dates conform well to our mtDNA evidence, which suggests that divergence occurred 4.2–5.9 Ma.

Taylor (1985) suggested that regional isolation of other marine-like mollusks was effected by inception of the southern reach of the freshwater Rio Grande in the Pleistocene, which disrupted and diluted an ancestral saline Pecos River (through which marine colonists dispersed). This assumes that the Pecos River was through-flowing to the Gulf prior to its integration with the Rio Grande and is supported by provenance interpretations of gravels on the Edwards Plateau and the lower Rio Grande (Thomas 1972, Belcher 1975). However, an analysis of river meander patterns suggests that the lower Pecos River early headed on the Edwards Plateau and did not integrate with the Pecos depression (where snails are endemic) until ca. 0.6 Ma, following incision of the Pecos Canyon through headward erosion (Amsbury & Dietrich 1987, Amsbury & Hayward 1999; also see Hills 1984:264). The occurrence of a fossil herring in the Gatuña Formation in southeastern New Mexico (Miller 1982), whose age is bracketed at 13–0.5 Ma (Powers & Holt 1993), suggests that marine biota may have been present in the region well prior to integration of the Pecos River drainage in conformance with our hypothesis. We agree with Taylor (1985) that marine-like Pleistocene gastropods from Terrell County, Texas (Andrews 1977:92,98,180) could have dispersed into this region along the ancestral lower Pecos River, however we attribute the Pleistocene occurrence of the brackish-water clam *Rangia cuneata* in the Pecos depression (Metcalf 1980, Taylor 1985, fig.

30) to dispersal along the same drainage system that was invaded by *Juturnia* progenitors.

Subsequent vicariance of *J. tularosae* estimated at 2.2–3.0 Ma (based on third position transitions only as there were no transversion changes at this position) is enigmatic in that geologic evidence suggests that Tularosa basin was endorheic during the Pleistocene and opened not to the east but to the south during the late Pliocene (5–2 Ma), when it served as a periodic tributary of the ancestral upper Rio Grande (Mack et al. 1996, 1997, Mack 1999). (Although pluvial Lake Otero [fide Herrick 1904] flooded Tularosa basin up to 1250 m elevation during its late Pleistocene highstand, it never breached its basin [Kottowski 1958, Miller 1981, Hawley 1993b, Pittenger & Springer 1999].) Any prior historical drainage relationship between this area and the Pecos region presumably was disrupted by late Tertiary extensional faulting, but is not well constrained as Tularosa basin, which consists of two adjacent deeply incised half-grabens (Lozinsky & Bauer 1991, Adams & Keller 1994), is bounded by mountain blocks which have had long uplift histories (Kelley & Chapin 1997) extending into the Quaternary (Machette 1987). The close relationship implied by our data between this component of the Rio Grande Rift and the southern Great Plains is paralleled by allozymic evidence of regional pupfishes (Echelle & Echelle 1992) and suggests a need for further study of the functionality of the regional drainage divide during the late Neogene.

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Literature Cited

- Abbott, R. T. 1958. The gastropod genus *Assimineia* in the Phillipines.—Proceedings of the Academy of Natural Sciences of Philadelphia 110:213–278.
- Adams, D. C., & G. R. Keller. 1994. Crustal structure and basin geometry in south-central New Mexico.—Geological Society of America Special Paper 291:241–255.
- Amsbury, D. L., & J. W. Dietrich. 1987. Some implications of incised meanders in the southern Edwards Plateau.—Geological Society of America Abstracts with Programs 19(3):115.
- , & O. T. Hayward. 1999. Quaternary erosional landscapes of central and North Texas.—American Association of Petroleum Geologists Annual Meeting Expanded Abstracts 1999:5.
- Andrews, J. 1977. Shells and shores of Texas, 2nd edition. University of Texas Press, Austin and London, 365 pp.
- Bachman, G. O. 1976. Cenozoic deposits of south-eastern New Mexico and an outline of the history of evaporite dissolution.—Journal of Research, U.S. Geological Survey 4:135–149.
- Bachuber, F. W., & W. A. McClellan. 1977. Paleogeology of marine Foraminifera in the pluvial Estancia Valley, central New Mexico.—Quaternary Research 7:254–267.
- Back, W., J. M. Lesser, & B. B. Hanshaw. 1977. Structural and stratigraphic occurrence of “bad water” in Coahuila, Mexico.—Geological Society of America Abstracts with Programs 9(7):885.
- Belcher, R. C. 1975. The geomorphic evolution of the

- Rio Grande.—Baylor Geological Studies Bulletin 29:1–64.
- , & W. E. Galloway. 1977. Evidence for early Tertiary Rio Grande drainage.—Geological Society of America Abstracts with Programs 9(1):5.
- Bowman, T. E. 1981. *Thermosphaeroma milleri* and *T. smithi*, new sphaeromatid isopod crustaceans from hot springs in Chihuahua, Mexico, with a review of the genus.—Journal of Crustacean Biology 1:105–122.
- Cather, S. M. 1991. Late Laramide paleodrainage patterns and timing of sedimentation in the southern Rocky Mountains and northwest Gulf of Mexico.—Geological Society of America Abstracts with Programs 23(4):10.
- Christiansen, R. L., & R. S. Yeats. 1992. Post-Laramide geology of the U.S. Cordilleran region. Pp. 261–406 in B. C. Burchfiel, P. W. Lipman, & M. L. Zoback, eds., The Cordilleran orogen, conterminous U.S. Geological Society of America, Boulder, 724 pp.
- Collins, T. M., K. Frazier, A. R. Palmer, G. J. Vermeij, & W. M. Brown. 1996. Evolutionary history of northern hemisphere *Nucella* (Gastropoda, Muricidae): molecular, morphological, ecological, and paleontological evidence.—Evolution 50: 2287–2304.
- Creel, G. C. 1964. *Hemigrapsus estellinensis*: a new grapsoid crab from north Texas.—Southwestern Naturalist 8:236–241.
- Echelle, A. A., & A. F. Echelle. 1992. Mode and pattern of speciation in the evolution of inland pupfishes in the *Cyprinodon variegatus* complex (Teleostei: Cyprinodontidae): an ancestor-descendant hypothesis. Pp. 691–709 in R. L. Mayden, ed., Systematics, historical ecology, and North American freshwater fishes. Stanford University Press, Stanford, 969 pp.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap.—Evolution 39:783–791.
- Frauenfeld, G. R. von. 1863. Vorläufige aufzählung der arten der gattungen *Hydrobia* Htm. Und *Amnicola* Gld. Hldm. In der kaiserlichen und in Cuming's sammlung.—Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wien 13:1017–1032.
- . 1865. Zoologische Miscellen.—Verhandlungen der Kaiserlich-Königlichen Zoologisch-botanischen Gesellschaft in Wien 15:525–536.
- Galloway, W. E., D. G. Bebout, W. L. Fisher, J. B. Dunlap Jr., R. Cabrera-Castro, J. E. Lugo-Rivera, & T. M. Scott. 1991. Cenozoic. Pp. 245–432 in A. Salvador, ed., The Gulf of Mexico Basin. Geological Society of America, Boulder, 568 pp.
- Gustavson, T. C., & R. J. Finley. 1985. Late Cenozoic geomorphic evolution of the Texas Panhandle and northeastern New Mexico—case studies of structural controls on regional drainage development.—Bureau of Economic Geology Report of Investigations 148:1–42.
- , & D. A. Winkler. 1988. Depositional facies of the Miocene-Pliocene Ogallala Formation, northwestern Texas and eastern New Mexico.—Geology 16:203–206.
- Hawley, J. W. 1993a. The Ogallala and Gatuña Formations in the southeastern New Mexico region, a progress report.—New Mexico Geological Society Guidebook 44th Field Conference: 261–269.
- . 1993b. Geomorphic setting and late Quaternary history of pluvial-lake basins in the southern New Mexico region.—New Mexico Bureau of Mines and Mineral Resources Open-File Report 391:1–28.
- Herrick, C. L. 1904. Lake Otero, an ancient salt lake basin in south-eastern New Mexico.—American Geologist 34:174–189.
- Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissooidea) of the Cuatro Ciénegas Basin, Coahuila, México.—Malacologia 26:31–123.
- . 1998. A systematic review of the hydrobiid snails (Gastropoda: Risssooidea) of the Great Basin, western United States. Part I. Genus *Pyrgolopsis*.—The Veliger 41:1–132.
- . 2001. Systematics of the North and Central American aquatic snail genus *Tryonia* (Rissooidea: Hydrobiidae).—Smithsonian Contributions to Zoology 612:1–53.
- , & W. F. Ponder. 1998. A review of morphological characters of hydrobioid snails.—Smithsonian Contributions to Zoology 600:1–55.
- , H.-P. Liu, & J. J. Landye. 2002. A new species of aquatic snail of the genus *Eremopyrgus* (Hydrobiidae: Cochliopinae) from the Chihuahuan Desert, Mexico: phylogenetic relationships and biogeography.—Journal of Molluscan Studies (in press).
- , & M. Mulvey. 1999. Phylogenetic relationships within the aquatic snail genus *Tryonia*: implications for biogeography of the North American Southwest.—Molecular Phylogenetics and Evolution 13:377–391.
- Hills, J. M. 1984. Sedimentation, tectonism, and hydrocarbon generation in Delaware Basin, west Texas and southeastern New Mexico.—American Association of Petroleum Geologists Bulletin 68:250–267.
- Holsinger, J. R. 1986. Zoogeographic patterns of North American subterranean amphipod crustaceans. Pp. 85–106 in R. H. Gore & K. L. Heck, eds., Crustacean biogeography. A.A. Balkema, Rotterdam & Boston, 292 pp.

- Horberg, L. 1949. Geomorphic history of the Carlsbad Caverns area, New Mexico.—*Journal of Geology* 57:464–476.
- Kelley, S. A., & C. E. Chapin. 1997. Cooling histories of mountain ranges in the southern Rio Grande rift based on apatite fission-track analysis—a reconnaissance survey.—*New Mexico Geology* 19(1):1–14.
- Kottowski, F. E. 1958. Lake Otero—second phase in formation of New Mexico's gypsum dunes.—*Bulletin of the Geological Society of America* 69:1733–1734. [abstract]
- Lesser, J. M., & G. Lesser. 1988. Region 9, Sierra Madre Oriental. Pp. 89–92 in W. Back, J. S. Rossenshein, & P. R. Seaber, eds., *Hydrogeology*. Geological Society of America, Boulder, 524 pp.
- Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology, part I: standard symbolic codes for institutional resource collections in herpetology and ichthyology.—*Copeia* 1985:802–832.
- Liu, H.-P., R. Hershler, & F. G. Thompson. 2001. Phylogenetic relationships of the Cochliopinae (Rissooidea: Hydrobiidae): an enigmatic group of aquatic gastropods.—*Molecular Phylogenetics and Evolution* 21(1):17–25.
- Lozinsky, R. P., & P. W. Bauer. 1991. Structure and basin-fill units of the Tularosa basin.—*New Mexico Geological Society 42nd Annual Field Conference*:7–11 (+ references).
- McVaugh, R. 1956. Edward Palmer, plant explorer of the American West.—University of Oklahoma Press, Norman, 430 pp.
- Machette, M. N. 1987. Preliminary assessment of paleoseismicity at White Sands Missile Range, southern New Mexico; evidence for recency of faulting, fault segmentation, and repeat intervals for major earthquakes in the region.—*United States Geological Survey Open-file Report* 87-0444:1–46.
- Mack, G. H. 1999. Neogene evolution of lakes and rivers in extensional basins of southwestern New Mexico.—*Geological Society of America Abstracts with Programs* 31(7):444.
- . 2001. Evolution of Cenozoic extensional block faulting and sedimentation in the southern Rio Grande Rift, New Mexico.—*Geological Society of America Abstracts with Programs* 33(5):47.
- , W. R. Seager, & W. C. McIntosh. 1996. Evolution of the southern Rio Grande Rift, south-central New Mexico.—*Geological Society of America Abstracts with Programs* 28(7):516.
- , D. W. Love, & W. R. Seager. 1997. Spillover models for axial rivers in regions of continental extension: the Rio Mimbres and Rio Grande in the southern Rio Grande rift, USA.—*Sedimentology* 44:637–652.
- Meinzer, O. E., & R. F. Hare. 1915. Geology and water resources of Tularosa basin, New Mexico.—*United States Geological Survey Water-Supply Paper* 343:1–317.
- Metcalf, A. L. 1980. Fossil *Rangia cuneata* (Mactridae) in Eddy County, New Mexico.—*Nautilus* 94:2–3.
- Miller, R. R. 1981. Coevolution of deserts and pupfishes (genus *Cyprinodon*) in the American Southwest. Pp. 39–94 in R. J. Naiman & D. L. Soltz, eds., *Fishes in North American deserts*. John Wiley & Sons, New York, 552 pp.
- . 1982. First fossil record (Plio-Pleistocene) of Threadfin Shad, *Dorosoma petenense*, from the Gatuña Formation of southeastern New Mexico.—*Journal of Paleontology* 56:423–425.
- , & A. A. Echelle. 1975. *Cyprinodon tularosa*, a new cyprinodontid fish from the Tularosa basin, New Mexico.—*Southwestern Naturalist* 19:365–377.
- Minckley, W. L. 1969. Environments of the Bolsón of Cuatro Ciénegas, Coahuila, México with special reference to the aquatic biota.—*University of Texas at El Paso Science Series* 2:1–65.
- , & G. A. Cole. 1968. Preliminary limnologic information on waters of the Cuatro Cienegas basin, Coahuila, Mexico.—*Southwestern Naturalist* 13:421–431.
- Miyamoto, S., L. B. Fenn, & D. Swietlik. 1995. Flow, salts, and trace elements in the Rio Grande: a review.—*Texas Water Resources Institute Technical Completion Report* TR-169:1–30.
- Morrison, J. P. E. 1945. *Durangonella*, a new hydrobiine genus from Mexico, with three new species.—*The Nautilus* 59:18–23.
- Ortiz, D., & K. M. Lang. 1996. Water resources data: New Mexico Water Year 1996.—*United States Geological Survey Water-Data Report* NM-95-1:1–446.
- , ———, & L. Beal. 1997. Water resources data: New Mexico water year 1997.—*United States Geological Survey Water-Data Report* NM-97-1:1–574.
- , ———, & ———. 1998. Water resources data: New Mexico water year 1998, vol. 1.—*United States Geological Survey Water-Data Report* NM-98-1:1–404.
- , ———, ———. 1999. Water resources data: New Mexico water year 1999, vol. 1.—*United States Geological Survey Water-Data Report* NM-99-1:1–402.
- Pittinger, J. S., & C. L. Springer. 1999. Native range and conservation of the White Sands Pupfish (*Cyprinodon tularosa*).—*Southwestern Naturalist* 44:157–165.
- Plummer, F. B. 1932 [1933]. Cenozoic systems in Tex-

- as. Pp. 519–818 in E. H. Sellards, W. S. Atkins, & F. B. Plummer, eds., *The geology of Texas*, vol. 1, *Stratigraphy*.—University of Texas Bulletin 3232:1–1007.
- Powers, D. W., & R. M. Holt. 1993. The upper Cenozoic Gatuña Formation of southeastern New Mexico.—*New Mexico Geological Society Guidebook 44th Field Conference*:271–282.
- Seemann, B. C. 1852–1857. *The botany of the voyage of the H.M.S. Herald, under the command of Captain Henry Kellett, R.N., C.B., during the years 1845–1851*.—Lovell Reeve, London, 483 pp.
- Seemann, B. 1853. *Narrative of the voyage of H.M.S. Herald during the years 1845–1851, under the command of Captain Henry Kellett, R.N., C.B.; being a circumnavigation of the globe and three cruises to the Arctic Regions in search of Sir John Franklin*. Two volumes. Reeve and Co., London, 623 pp.
- Smith, M. L., & R. R. Miller. 1986. The evolution of the Rio Grande basin as inferred from its fish fauna. Pp. 457–485 (+ references) in C. H. Hocutt & E. O. Wiley, eds., *The zoogeography of North American freshwater fishes*. John Wiley & Sons, New York, 866 pp.
- Stockwell, C. A. & M. Mulvey. 1998. Phosphoglucuronate dehydrogenase polymorphism and salinity in the White Sands pupfish.—*Evolution* 52: 1856–1860.
- Strain, W. S. 1966. Blancan mammalian fauna and Pleistocene formations, Hudspeth County, Texas.—*Bulletin of the Texas Memorial Museum* 10:5–55.
- Swofford, D. L. 1998. PAUP*: phylogenetic analysis using parsimony (and other methods). Version 4.0. Sinauer Associates, Sunderland, Massachusetts.
- Taylor, D. W. 1966. A remarkable snail fauna from Coahuila, México.—*The Veliger* 9:152–228.
- . 1985. Evolution of freshwater drainages and molluscs in western North America. Pp. 265–321 in C. J. Smiley, ed., *Late Cenozoic history of the Pacific Northwest, interdisciplinary studies on the Clarkia fossil beds of northern Idaho*. American Association for the Advancement of Science, San Francisco, 417 pp.
- . 1987. Fresh-water mollusks from New Mexico and vicinity.—*New Mexico Bureau of Mines & Mineral Resources* 116:1–50.
- Thomas, R. G. 1972. The geomorphic evolution of the Pecos River system.—*Baylor Geological Studies Bulletin* 22:1–40.
- Troschel, F. H. 1856–1863. *Das gebiss der schnecken zur begründung einer natürlichen classification*, vol. 1. Nicolaische Verlagsbuchhandlung, Berlin, 252 pp.
- Tryon, G. W. 1866. [Review of] *Researches upon the Hydrobiinae and allied forms*.—*American Journal of Conchology* 2:152–158.
- Winker, C. D. 1982. Cenozoic shelf margins, northwestern Gulf of Mexico.—*Gulf Coast Association of Geological Societies Transactions* 32: 427–448.